Genetic Relationships of Elwha River *Oncorhynchus mykiss* to Hatchery-Origin Rainbow Trout and Washington Steelhead

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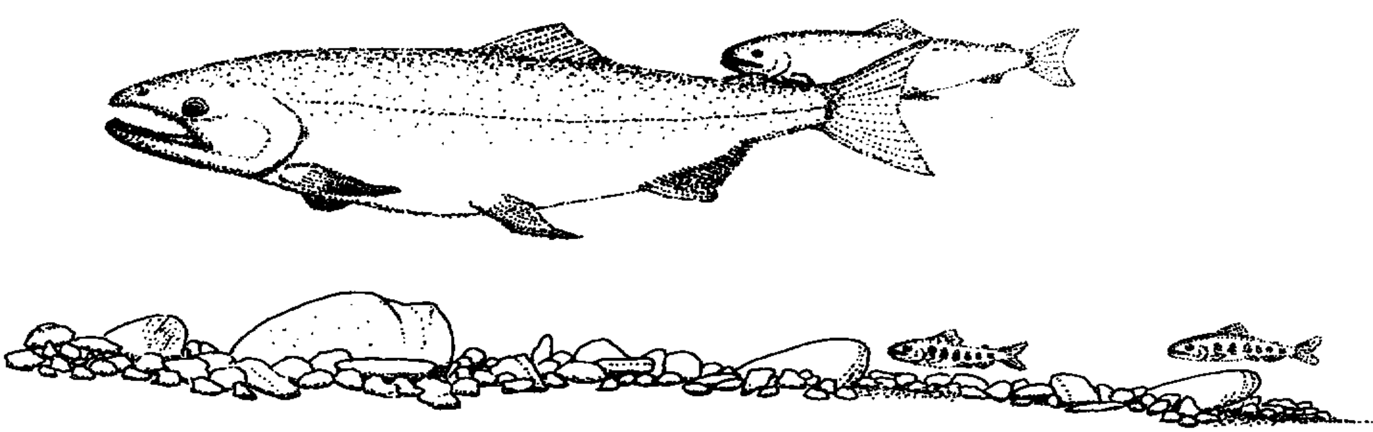

Genetic Relationships of Elwha River *Oncorhynchus mykiss* to Hatchery-Origin Rainbow Trout and Washington Steelhead

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Abstract

We used allozyme electrophoresis to determine the ancestry of rainbow trout, *Oncorhynchus mykiss,* from seven locations in the Elwha River Basin. *O. mykiss* in these areas have been isolated from anadromous steelhead since the early 1900's by two mainstem dams. Elwha River rainbow trout, the resident form of *O. mykiss*, may be descendants of native rainbow trout, native steelhead, or these fish may be derived from the numerous plants of hatchery-origin rainbow trout and cutthroat trout, *O. clarki*, that have occurred in the Elwha River. The pending removal of both dams will re-establish anadromous fish access to the watershed. The current anadromous fish restoration strategy recommends that hatchery-reared juvenile salmonids be released into the river upstream of the dams to accelerate re-colonization of these habitats. This strategy requires the identification of viable broodstock sources. We compared the genetic profiles of *O. mykiss* from seven collection sites within the Elwha River Basin to allozyme characteristics of hatchery-origin rainbow trout strains, hatchery and natural populations of Washington steelhead, and cutthroat trout subspecies, to help guide decisions on anadromous fish restoration. Native Washington *O. mykiss* and hatchery-origin rainbow trout can be differentiated using allozymes because the commonly used hatchery rainbow trout strains originated from California. These rainbow trout strains contain genetic variation that has not been identified in native Washington steelhead populations. Cutthroat trout subspecies also contain distinct genetic variation.

Evidence of successful natural reproduction by hatchery-origin rainbow trout was observed in all collections except the one from the South Fork Little River (a lower Elwha River tributary). Estimates of alleles derived from hatchery rainbow trout were 0% in the South Fork Little River collection, less than 5% in the upper Elwha River, and 5% - 20% in the remaining sampling locations. It appears that the hatchery rainbow trout gene pool has mixed with the native *O. mykiss* in many areas based on the distribution of alleles. Cutthroat trout and rainbow x cutthroat hybrids were rare.

The genetic attributes of all the *O. mykiss* collections in the Elwha River were significantly different from both hatchery and natural populations of Washington steelhead. Based on genetic distance relationships, all the collections, except for the South Fork Little River, clustered together. The *O. mykiss* population from the South Fork Little River was most closely related to Washington steelhead collections. But, the fish from this location had the lowest levels of genetic variation.

The South Fork Little River *O. mykiss* population should be examined further to determine if its life history pattern supports genetic evidence that this population represents landlocked descendants of native Elwha River steelhead. Additional locations, especially the upper watershed and other tributaries, should be examined to determine if additional broodstock sources are available to increase the overall genetic diversity of the broodstock. This is important due to the apparent reproductive isolation observed in this study.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The Elwha River, which has its headwaters in the Olympic National Park and flows into central Strait of Juan de Fuca, was a major salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) producer in this region of Washington. Dams at river kilometer (Rkm) 9 and 21 have blocked all upstream fish migration since 1914. Now these dams may be removed and access for anadromous fish to a large portion of the watershed restored. The Elwha River Ecosystem and Fisheries Restoration Act (Public Law 102-495; section 3(d)) of 1992 established the goal of full restoration of the Elwha River's ecosystem and native anadromous fish runs. As part of the anadromous fish restoration in the Elwha River, Federal, State, and Tribal fishery agencies are considering plans to accelerate re-colonization by releasing hatchery-reared juvenile salmonids into the river upstream of the existing dam sites for 8 to 10 years after safe fish passage is assured (Wunderlich et al. 1994). One requirement of this restoration strategy is the identification of the best sources of salmonid broodstocks.

Steelhead are a candidate species for hatchery-assisted restoration in the Elwha River (Wunderlich et al. 1994). The non-anadromous (resident) form of this species, rainbow trout, in the Elwha River may be descendants of native steelhead and could be used as broodstock for restoration. Rainbow trout from the upper Elwha River (upstream of Rkm 32) may represent native Elwha River steelhead (Reisenbichler and Phelps 1989). However, limited numbers of upper Elwha rainbow trout, combined with difficult logistics for fish capture, make broodstock collection in this area very difficult. The presence of downstream migrants approximately 1 km downstream of Glines Canyon Dam (Figure 1) which appear to be smolting and are adaptable to saltwater (Winchell 1991; Hiss and Wunderlich 1994), provides an opportunity to capture fish in relatively accessible lower and middle Elwha River locations. These fish could be reared in captivity and used as broodstock upon maturing. But, there are potential problems with using these fish as broodstock because non-local hatchery-origin rainbow trout and non-local cutthroat trout, *O. clarki,* subspecies have been stocked in the Elwha River. In addition, resident forms of native coastal cutthroat trout are found above the dams. All of these fish are known to interbreed and produce viable progeny. This raised concerns that lower and middle Elwha River trout may not represent native Elwha River steelhead.

Hatchery-origin rainbow trout were stocked into waters containing wild populations based on the assumption that it would enhance recreational fisheries. Incomplete stocking records that we obtained indicate that the Elwha River was routinely planted with rainbow trout from numerous Federal hatcheries and the State of Washington's Goldendale Hatchery for many years. These plants into the Elwha River have now ceased. The ancestry of rainbow trout strains from most of the Federal hatcheries (Busack and Gall 1980; Dollar and Katz 1964) and all four of the Washington Department of Fish and Wildlife (WDFW) State hatcheries (Crawford 1979) can be traced to the McCloud River in California.

These California-origin hatchery rainbow trout strains have characteristic alleles (Busack et al.

1979; Milner et al. 1979; Kincaid 1980) that have not been found in native rainbow trout and steelhead populations in Washington (Phelps 1993; Phelps et al. 1994). The presence of these alleles in the current Elwha River Basin rainbow trout populations would be an indication of successful natural reproduction of stocked hatchery rainbow trout. Thus, these alleles can be used to determine if the present rainbow trout populations were derived primarily from native rainbow trout and/or residual steelhead, the offspring of hatchery-origin rainbow trout and/or cutthroat trout, or a mixture of hatchery and native fish. We refer to allelic markers that are characteristic of California-origin rainbow trout hatchery strains as "hatchery alleles". However, this does not indicate that they originated as part of fish culture or are the result of domestication selection, although their frequencies may have changed substantially over the years as a result of hatchery propagation.

Few studies have examined the genetic contribution of hatchery-origin trout to wild populations. Reisenbichler and Phelps (1989) determined that a single collection of rainbow trout from the upper Elwha River was more similar to Olympic Park steelhead than to several stocks of hatchery rainbow trout. Campton and Johnson (1985) found evidence of interbreeding between wild and hatchery trout in the Yakima River. Further work by Phelps (1993) and Phelps and Baker (1994) indicated that the amount of interbreeding was quite variable among different locations in the Yakima River. In the upper river and tributaries above Cle Elum, the introgression was low, but in the mainstem and tributaries near Ellensburg, over half the gene pool was estimated to be hatchery derived. Taggart and Ferguson (1986) also found introgression of hatchery and native brown trout (*Salmo trutta*) stocks in Northern Ireland after 15 years of supplemental stocking. The percentage of hatchery-origin genetic contribution varied widely from river to river (19%-91%). However, Marnell et al. (1987) found native populations of westslope cutthroat trout (*O. clarki lewisi*) in lakes within Glacier National Park, Montana, after the stocking of rainbow trout and Yellowstone cutthroat trout (*O. clarki bouveri*) into these waters. In addition, Currens (1987) and Currens et al. (1990) found little evidence of nonnative hatchery genes in stocked rainbow trout populations in the Deschutes River, Oregon.

There have been few direct comparisons of known rainbow trout populations to known steelhead populations from the same locations in Washington. Typically, the portions of streams in western Washington that have access to marine waters have had relatively few resident rainbow trout compared to the anadromous steelhead. However, WDFW biologists have identified locations where both resident and anadromous fish were thought to occur. Contradictory results have been obtained from these limited comparisons. Phelps et al. (1997) found evidence of genetic isolation in juveniles (n = 15) from the Hamma Hamma River classified as anadromous and resident based on otolith strontium levels. In contrast, Berejikian et al. (2001) found no evidence of genetic isolation of resident and anadromous fish from the Hamma Hamma River below an anadromous barrier. However, resident fish above the barrier were distinct from resident and anadromous fish below the barrier (Berejikian et al. 2001). Resident and anadromous fish within the Yakima River Basin were not distinct (Phelps et al. 2000). One hypothesis explaining the lack of genetic divergence in sympatric resident and anadromous populations of *O. mykiss*, is that anadromy and residency is just natural variation within a population, similar to different ages of maturation or return timing.

The three general objectives of this study were to:

1) Determine the level of genetic similarity among *O. mykiss* collections from the Elwha River. The null hypothesis is that there is no difference in the allozyme characteristics among *O. mykiss* from the seven collection areas. We did this test to determine whether or not broodstock for anadromous fish restoration could be taken from throughout the Elwha River. Access to much of the watershed is difficult because of the terrain.

2) Estimate the contribution of hatchery-origin rainbow trout or cutthroat trout to the present *O. mykiss* gene pools at each collection location. The null hypothesis is that the allelic composition of Elwha River rainbow trout collections are not different from the allelic composition of the four Washington hatchery rainbow trout strains. The degree of similarity to hatchery rainbow trout can be estimated by the ratio of specific alleles that are characteristic of hatchery rainbow trout used in Washington. We also wanted to determine if cutthroat trout have interbred with the rainbow trout and to exclude such fish from the analyses.

3) Determine the genetic similarity of Elwha River *O. mykiss* collections to naturally-produced and hatchery winter-run and summer-run Olympic drainage steelhead populations. The null hypotheses are that the genetic characteristics of the Elwha River collections do not differ significantly from naturally produced steelhead collected from Olympic Peninsula and coastal Washington streams, and from hatchery steelhead strains used for many years by WDFW. We performed these tests to help guide the determination of broodstock sources that may be suitable for steelhead restoration. In addition to genetic distance, we compared the levels of genetic variation found in the Elwha River *O. mykiss* to levels found in wild and hatchery steelhead collections.

METHODS

O. mykiss were collected from seven general locations in the Elwha River Basin (Figure 1). Samples from several sites within each general location were combined into one "collection". Collections were obtained from one location in the Elwha River Basin in 1993 and five locations in 1994 (Figure 1). Data for one collection from a previous study in 1983 were also used in some analyses. Rainbow trout (n=50) from the previous study (1983) came from a collection in the upper Elwha River (upper Elwha River in this report refers to the area above Lake Mills) near the Hayes River and Godkin Creek in 1983 (Figure 1) (Reisenbichler and Phelps 1989). Resident fish were collected in the Little River mainstem (n=14), Indian Creek (n=36), South Fork Little River (n=50), and Lake Mills (n=55) and smolts were captured below Glines Canyon Dam (n=20) in 1994. Sampling methods and locations have been discussed in detail by Hiss and Wunderlich (1994). The 1993 collection (n=60) was from the upper mainstem Elwha River near Press Valley (by J. Meyer, Olympic National Park). Steelhead data were from Phelps et al. (1994) and unpublished WDFW records. There have been no other wild rainbow trout collections in western Washington that could be used for comparisons. Hatchery rainbow trout data came from Reisenbichler and Phelps (1989) and Phelps (1993).

Muscle, heart, eye, and liver were dissected from each fish and electrophoresis was performed following the methods of Aebersold et al. (1987) and Phelps et al. (1994). The electrophoretic protocol, enzymes screened, and alleles observed during this study and other studies on rainbow trout and steelhead by WDFW are listed in Phelps et al. (1994). Genetic nomenclature follows the conventions of Shaklee et al. (1990), and laboratory data management was described by Shaklee and Phelps (1990). Each fish was assayed for genetic variation at 92 loci. Fifty-six of these loci were chosen for the analysis based on enzyme activity, resolution, and the presence of genetic variation in Washington steelhead and hatchery-origin rainbow trout.

All *O. mykiss* collected in 1994 from the Elwha River were aged to determine if different year classes contributed to the fish collections. Scales were scraped off the dorsal side of the trout using a blunt knife and placed on scale cards for pressing at a later date. Scales were pressed on a slide using a hydraulic press and aged using standard methods (Jearld 1983).

Data Analysis

Allelic data from electrophoretic assays are typically evaluated and analyzed in a variety of ways to meet specific study objectives. A detailed description of the specific steps, rationale, and assumptions used in these analyses was presented by Phelps et al. (1994). Data analyses for this study focused on genetic similarities of collections and, identification and estimation of the presence and magnitude of hatchery-origin alleles. For fuller treatment of genetic analyses applicable to fisheries management in general, see Ryman and Utter (1987) and Whitmore (1990).

We tested the genetic similarity among *O. mykiss* collections from the Elwha River using the G-statistic. We tested the null hypothesis that the allele frequencies at variable loci in two collections were no different from what would be expected from two samples from a single random mating population (of the same sample size as the collections being compared). All possible pairs of collections were tested with two different numbers of loci. The 1993 and 1994 collections were compared at the 35 variable loci identified in this study. These recent collections were compared to the 1983 collection of Reisenbichler and Phelps (1989) at 18 loci (these 18 loci were variable in at least one population and in common between both studies). These multiple paired tests were not corrected using the Bonferroni correction.

We estimated the contribution of past hatchery rainbow trout plants to the present *O. mykiss* gene pools for each collection from the Elwha River, by comparing the frequency of specific alleles at five loci, to the frequencies from a composite of WDFW rainbow trout strains. Data from numerous Washington steelhead collections and from Oregon (Currens 1987) suggest that alleles at the following five loci were derived from California-origin hatchery rainbow trout: *ADA-1*85*

*(0.80), CK-A1*67(0.06), mIDHP-2*144(0.37), LDH-C*95(0.10), PGM-2*85(0.04).* The allele frequencies used for the comparison are in parentheses following the locus name. We presumed that these alleles did not occur in the Elwha River prior to the stocking of hatchery rainbow trout (frequency = 0.00). Although there was heterogeneity among the hatchery strains, we chose to make a composite of hatchery rainbow trout genetic characteristics as a representative hatchery strain for the estimation of hatchery introgression. We did this because a variety of different rainbow trout strains of California origin have been planted into the Elwha River (USFWS, unpublished data). Other alleles that are common in hatchery rainbow trout of California origin are *CK-C1*105, bGLUA*77, bGLUA*85, sIDHP-2*123, and sMDH-B1,2*85.* The frequencies of these alleles vary substantially among hatchery strains due to the long-term culture of these fish. Therefore, these alleles were not used in the estimation of hatchery introgression.

Various computer programs were used to analyze the electrophoretic data for this study. BIOSYS-1 (Swofford and Selander 1981) was used to calculate allele frequencies, average heterozygosities, percentages of polymorphic loci, average number of alleles per locus, genetic distances, and heterogeneity chi-square tests of allele counts. A program that performs log-likelihood ratio tests (G-statistic) (Sokal and Rohlf 1981), written by Craig Busack (WDFW), was used to test for significant differences in allele frequencies between pairs of collections. NTSYS-PC (Rohlf 1992) was used to graphically represent some of the genetic distance relationships. We used the genetic chord distance measure of Cavalli-Sforza and Edwards (1967) and Nei's unbiased genetic distance (Nei 1978) to generate dendrograms (using the unweighted pair-group method with arithmetic averaging, UPGMA) and multidimensional scaling diagrams (Rohlf 1992) to illustrate relationships among collections. Examination of collections for gametic disequilibrium was conducted using a program (PANMIX) written by Don Campton (University of Florida/USFWS). Many of the above programs were modified by Craig Busack and Chris Marlowe (both of WDFW) to accept data input in a standardized format, and to provide improved output formats.

RESULTS

All the allelic variation observed in the Elwha River collections has been found in other steelhead and rainbow trout populations, and cutthroat trout subspecies (i.e., no unique alleles were identified in this study). The following loci did not express any electrophoretically detectable variation in the collections from the Elwha River: *sAAT-3; mAH-1; mAH-2; mAH-3; CK-A1; CK-A2; GAPDH-3; GPI-A; GPI-B1; GPI-B2; IDDH-1; mIDHP-1; LDH-A1; LDH-B1; sMDH-A1,2; MPI; PGM-1; PGM-1r; PNP; mSOD.*

Three individual fish in this study were judged to be cutthroat trout or cutthroat x rainbow hybrids based on the presence of cutthroat trout-specific alleles (Leary et al. 1987; Phelps, unpublished data). Two fish were dropped from the Indian Creek collection and one fish from the Lake Mills collection because cutthroat trout alleles were found at a frequency ≥ 50% (fish 94BX13 was a pure westslope cutthroat trout, fish 94BX31 was a cutthroat trout hybrid, and fish 94BY39 was a hybrid coastal cutthroat trout). No other cutthroat trout were observed in any of the other collections.

Similarity Within Elwha River Collections

A majority of pair-wise comparisons of allele frequencies were significantly different, even though the sample sizes were small (Table 1). The paired combinations of Indian Creek with the mainstem Little River and Glines Canyon Smolts were not significantly different from each other using 18 and 35 loci. The mainstem Little River and Glines Canyon smolts were not significantly different from each other using 35 loci, but were marginally different using 18 loci ($0.01 < P < 0.05$). The Lake Mills collection was not significantly different from the Glines Canyon smolts at the 18 loci, but was marginally different ($0.01 < P < 0.05$) using 35 loci. The 1993 upper Elwha River collection and the South Fork Little River were significantly different from all other collections ($P < 0.001$). The only collection not different at the $P < 0.001$ level with the 1983 collection was the Glines Canyon smolts. These results indicate that there is reproductive isolation between some *O. mykiss* populations within the Elwha River and tributaries.

We illustrated the genetic distance relationships of Elwha River rainbow trout collections to each other using a dendrogram (Figure 2). The South Fork Little River was an outlier relative to the other populations. The 1983 and 1993 upper river collections grouped with one another before grouping with any of the lower river populations. A close relationship of Indian Creek with the Little River mainstem was also observed.

Similarity to Hatchery Strains

All the *O. mykiss* collections from the Elwha River were significantly different ($P < 0.0001$) from WDFW hatchey rainbow trout strains. However, alleles characteristic of hatchery-origin rainbow trout were observed at some locations. We found evidence of successful breeding of hatchery rainbow trout in all collections except the South Fork Little River. The absence of hatchery-origin rainbow trout alleles is one explanation for why *O. mykiss* collections from the South Fork Little River had the largest genetic distances compared to the other Elwha River collections (Figure 2). The estimated percent of alleles derived from hatchery rainbow trout was less than 5% in the upper Elwha River (1993), and between 5% - 20% in the other locations.

The identification of alleles characteristic of hatchery rainbow trout in collections could be due to the presence of a few pure hatchery fish in a collection of pure wild fish; or it could indicate that interbreeding has occurred (introgression). It's important to determine which of these two possibilities resulted in the presence of hatchery alleles in our samples. If the gene pools have remained distinct, then pure wild fish could be sorted out from the hatchery fish for broodstock collection. The characteristic hatchery rainbow trout alleles would be randomly mixed throughout the sample of fish in the collections if hatchery and wild fish have been interbreeding for many generations. If there has been reproductive isolation between hatchery-origin and native fish, the hatchery-origin alleles would tend to be associated with one another, and conversely, native alleles would be associated with other native alleles. In this latter case, there would tend to be a deficit of heterozygotes compared to the expected Hardy-Weinberg genotype proportions, and significant gametic disequilibrium would be present. We used these two measures to determine if we could detect nonrandom mating. We used loci that had at least five variable alleles (excluding the isoloci) for the Hardy-Weinberg genotype equilibrium tests. Two loci out of the 48 tests were significantly different at the 0.05 criterion level, which is about what would be expected by chance. We also could not detect any gametic disequilibrium in any of the six collections. Thus, the evidence suggests that the hatchery rainbow trout gene pool has mixed with the native fish.

The mean number of alleles per locus, the proportion of loci that are polymorphic in each collection at the 0.01 and 0.05 criteria, and two measures of heterozygosity based on 56 loci for each collection and selected Washington steelhead collections are presented in Table 2. The two locations with the least hatchery rainbow trout hybridization (S. Fork Little River and upper Elwha River 1993) also had the lowest genetic variability based on percentage of loci polymorphic at the 0.05 criterion level and mean heterozygosity, when compared to other Elwha River collections. These two sites were also among the lowest when compared to other Washington steelhead populations (Collections 7-30; Table 2).

Similarity to Other Olympic Steelhead

The overall allele frequencies of all the Elwha River *O. mykiss* collections were significantly different from both hatchery and wild steelhead collections from coastal Washington based on paired G-tests. We used a UPGMA dendrogram (Figure 3) to display the genetic distance relationships among the Elwha River *O. mykiss* and some selected Washington steelhead populations. We used 56 loci and the unbiased genetic distance measure of Nei (1978) (these loci are a standard subset of the coast wide steelhead data set). On the dendrogram, the South Fork Little River collection was most closely related to that from the East Fork Humptulips River, and grouped with most other steelhead populations before clustering with the other Elwha River populations.

The genetic distances between the South Fork Little River and wild winter-run steelhead collections in many cases were smaller than the distances to the Chambers Creek (0.0030) and Bogachiel (0.0054) hatchery winter-run steelhead. Some examples of genetic distance between the South Fork Little River collection and wild winter-run steelhead were: East fork Humptulips (0.0008), North River (0.0011), Humptulips (0.0014), Calawah (0.0016), and Nemah (0.0016). Genetic distances to several other Strait of Juan de Fuca streams were: Hoko (0.0019), Morse

(0.0023), Pysht (0.0024), and Dungeness (0.0029). However, some WDFW biologists suspect that these Strait of Juan de Fuca streams have had some successful natural production of Chambers Creek-origin winter-run steelhead (Phelps 1997).

The other Elwha River collections were more closely related to each other than to the bulk of Washington steelhead populations. The 1983 collection from the upper Elwha River was dropped from this genetic distance analysis because we wanted to use the larger locus data set. A similar pattern occurred on the multidimensional scaling plot (Figure 4). The South Fork Little River (4SFKLit) fell among the Washington steelhead collections and the Glines Canyon smolts were intermediate between Washington steelhead and the other Elwha River collections.

Age Structure of Elwha River Collections

The number of fish from each age class in the 1994 collections varied among sites (Table 3). At least two age-classes were represented in all collections except those from Glines Canyon, in which only 2-year-old fish were observed. Rainbow trout sampled from Lake Mills had the greatest range of ages, with age classes from 1+ to 5+ represented. Indian Creek, the mainstem of Little River, and South Fork Little River had only 1+ and 2+ year-old fish represented in the sample. The average size of fish from different age classes and different sampling locations is presented in Figure 5.

DISCUSSION

Since the first dam on the Elwha River was constructed in 1910, steelhead have been prevented from ascending into the areas where we collected rainbow trout. Reisenbichler and Phelps (1989) listed three possibilities for the origin of the present populations of rainbow trout in the Elwha River. The first possibility was that they developed from native rainbow trout and/or steelhead, and that the present allele frequencies developed from genetic drift and natural selection. The second possibility was that they descended from only hatchery rainbow trout. The final possibility was that a landlocked steelhead population developed but subsequently has interbred with hatchery rainbow trout.

In five of the locations where we collected rainbow trout, hatchery rainbow trout apparently have had limited success at reproducing in the wild, but have interbred with native Elwha River *O. mykiss*. We found no evidence of hatchery rainbow trout origin genes in the collection from the South Fork Little River. This population was also more similar to Olympic steelhead than to hatchery steelhead. However, this population has less genetic variation than other Elwha *O. mykiss*, and wild and hatchery steelhead. This is most likely the result of genetic drift due to small numbers of breeding adults over time.

The apparent similarity to Olympic steelhead and lack of characteristic hatchery-origin rainbow trout alleles suggest that the South Fork Little River could potentially represent native Elwha steelhead. However, electrophoretic information from this analysis is based on only two age-classes (1+ and 2+). Reisenbichler and Phelps (1989) observed significant variation in allele frequencies among different year-classes of native Olympic steelhead, suggesting that several year-classes of fish should be used for genetic characterization studies. Although only two age-classes are represented in this analysis, the lack of hatchery alleles in both age-classes suggests that hatchery rainbow trout have not interbred with this population.

O. mykiss from the South Fork Little River could potentially represent native Elwha steelhead and it is suggested that further investigations be completed for this population. The goal of any broodstock program would be to use a stock most likely to succeed in the environment into which their progeny will be planted. A native brood population is advantageous because it has persisted and evolved within the drainage. However, genetic changes may have occurred in this population, since the population has persisted without the marine phase of its life history. This may limit their usefulness as a brood source, if these changes impact the population's ability to survive the marine phase of its life history. Life history investigations should be completed to determine if this population provides a viable brood source, especially given the observation that the genetic variation observed in *O. mykiss* from the South Fork Little River collection was the lowest observed during this study. These studies should include the examination of emigration behavior (smolt migration) and adaptability to seawater.

The lack of older age-classes in the South Fork Little River collection could be caused by movement of older fish into larger streams or lakes (Peven et al. 1994; Pearsons et al. 1994) or emigration of smolts. Downstream migrants (smolts) caught in a scoop trap located in Glines Canyon were all age 2+ and were adaptable to seawater (Hiss and Wunderlich 1994). These smolts were larger than the age 2+ fish present in the South Fork Little River, suggesting that age 2+ fish present in the South Fork Little River may not have obtained sufficient size for smoltification during the previous spring. There is currently inadequate information to determine if smoltification or lack of habitat for older (larger fish) age-classes is responsible for the lack of older age-classes in this system. The presence of only 1+ and 2+ age-classes in the mainstem Little River and Indian Creek and older (3-5) age-classes in Lake Mills supports both theories. Some smolts may residualize in the reservoirs rather than completing their migration to sea (Dilley and Wunderlich 1987; Wunderlich et al. 1989). However, limited instream habitat for older and larger non-anadromous fish may also cause older-age classes to be present in Lake Mills and younger-age classes to be present in the tributaries. Downstream migrant data and subsequent salt water challenge information for emigrants are required to determine the factors responsible for only 1+ and 2+ year-old fish present in the South Fork Little River collection.

The South Fork Little River would be a relatively good location for broodstock collection; if further studies determine that the fish from this area have suitable life-history characteristics (e.g., ability to adapt to saltwater). This stream had one of the highest catch rates of the five 1994 sampling locations and access is relatively good compared to other locations in the Elwha

River basin. Estimates of population size would be required to determine the best approach for broodstock collection (i.e., eyed-egg, presmolt, smolt, or adult).

Many options exist for restoration of naturally-produced, self-sustaining steelhead in the Elwha River. The use of resident rainbow trout may increase the likelihood of successful restoration. In contrast, adaptation to a resident life history for many years may have diminished the ability to become a successful anadromous population. The identification of a location in the Elwha River Basin that appears to have *O. mykiss* similar to wild populations of western Washington steelhead was the first step to determining if viable broodstock sources are available for restoration.

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Table 1. Results of pair-wise G-tests of allele frequencies using 35 variable loci (above diagonal) and 18 loci (below diagonal) between rainbow trout collections from the Elwha River. The top row lists the sample size for each site. Cells that contain a 0 are significant at $P < 0.001$. Other cells have their significance level indicated. NS= not significant. An @ sign in a cell indicates that a test could not be done because fewer loci were assayed in the 1983 collection. Note that significance levels were not corrected for multiple tests using the Bonferroni correction.

	Upper Elwha 1983	Upper Elwha 1993	Indian Creek 1994	Lake Mills 1994	South Fork Little River 1994	Little River 1994	Glines Canyon 1994
n	50	60	36	55	50	14	20
Upper Elwha 1983		@	@	@	@	@	@
Upper Elwha 1993	0		0	0	0	0	0
Indian Creek 1994	0	0		0	0	NS	NS
Lake Mills 1994	0	0	0.05		0	0	0.05
South Fork Little River 1994	0	0	0	0		0	0
Little River 1994	0	0	NS	0.01	0		NS
Glines Canyon 1994	0.01	0	NS	NS	0	0.05	

Table 2. Genetic variability within steelhead and rainbow trout collections, measured at 56 loci.

Collection[1]	Mean No. of alleles per locus	Percentage of loci polymorphic at 0.01 level	Percentage of loci polymorphic at 0.05 level	Mean hetererozygosity: Direct count	Mean hetererozygosity: Hardy-Weinberg expected
Elwha River Rainbow Trout					
1. UPElwha93	1.5	32.1	12.5	0.050	0.053
2. IndianCR94	1.7	42.9	21.4	0.079	0.079
3. LkMills94	1.6	32.1	19.6	0.073	0.071
4. SFKLittleR94	1.3	26.8	12.5	0.046	0.051
5. LittleRMS94	1.4	23.2	19.6	0.082	0.078
6. GlinesCan94	1.6	35.7	16.1	0.067	0.070
Steelhead					
7. Skamania FH 93WR	1.5	37.5	16.1	0.063	0.064
8. Chambers Cr FH 93WR	1.7	51.8	19.6	0.078	0.079
9. Bogachiel FH 93WR	1.6	44.6	21.4	0.081	0.080
10. Skamania FH 94SR	1.5	41.1	19.6	0.069	0.067
11. Hoko R 94	1.7	42.9	17.9	0.072	0.076
12. Dungeness R 94	1.5	37.5	19.6	0.066	0.068
13. Skokomish R 94	1.5	41.1	16.1	0.075	0.068
14. Tahuya R 94	1.6	55.4	17.9	0.084	0.082
15. Sitkum R 94	1.6	42.9	16.1	0.069	0.072
16. Humptulips 94	1.7	53.6	19.6	0.078	0.080
17. Wynooche 94	1.6	41.1	16.1	0.075	0.072
18. Satsop 94	1.4	32.1	19.6	0.072	0.067
19. Naselle 94	1.5	35.7	17.9	0.066	0.071

Table 2. (Continued)

Collection[1]	Mean No. of alleles per locus	Percentage of loci polymorphic at 0.01 level	Percentage of loci polymorphic at 0.05 level	Mean heterozygosity	
				Direct count	Hardy-Weinberg expected
20. Nemah 94	1.4	35.7	14.3	0.070	0.066
21. Sol Duc 94	1.6	39.3	21.4	0.079	0.074
22. Bogachiel 94	1.7	44.6	25.0	0.089	0.088
23. Calawah 94	1.5	37.5	16.1	0.071	0.068
24. Dosewallips 94	1.6	35.7	17.9	0.074	0.073
25. Morse Cr 94	1.7	46.4	23.2	0.079	0.079
26. Pysht 94	1.5	37.5	19.6	0.078	0.079
27. EFHumptulips 94	1.5	35.7	21.4	0.065	0.074
28. WFHumptulips 94	1.4	39.3	19.6	0.071	0.074
29. North 94	1.6	42.9	19.6	0.075	0.074
30. Stillman 94	1.4	30.4	17.9	0.069	0.071
WDFW Hatchery Rainbow Trout					
31. Spokane FH 90	1.5	35.7	19.6	0.094	0.085
32. Goldendale FH 90	1.4	30.4	23.2	0.087	0.084
33. S Tacoma FH 90	1.4	32.1	23.2	0.095	0.093
34. Tokul CR FH 90	1.2	21.4	17.9	0.076	0.074

[1]Number next to collection site is used in Appendix A to reference collection numbers to collection locations.

Table 3. Numbers of rainbow trout sampled from each age class in the 1994 collections.

Location	Age Classes 1	2	3	4	5
Glines Canyon	0	22	0	0	0
Indian Creek[1]	12	17	3	0	0
Lake Mills[2]	2	27	16	5	2
Little River	6	7	0	0	0
S.F. Little River	41	6	0	0	0

[1]Age of two additional fish not determined. They appear to be 3 year olds based on size.
[2]Age of three additional fish not determined. Based on size they appear to be 2 (one), 3 (one), and 5 (one) years old.

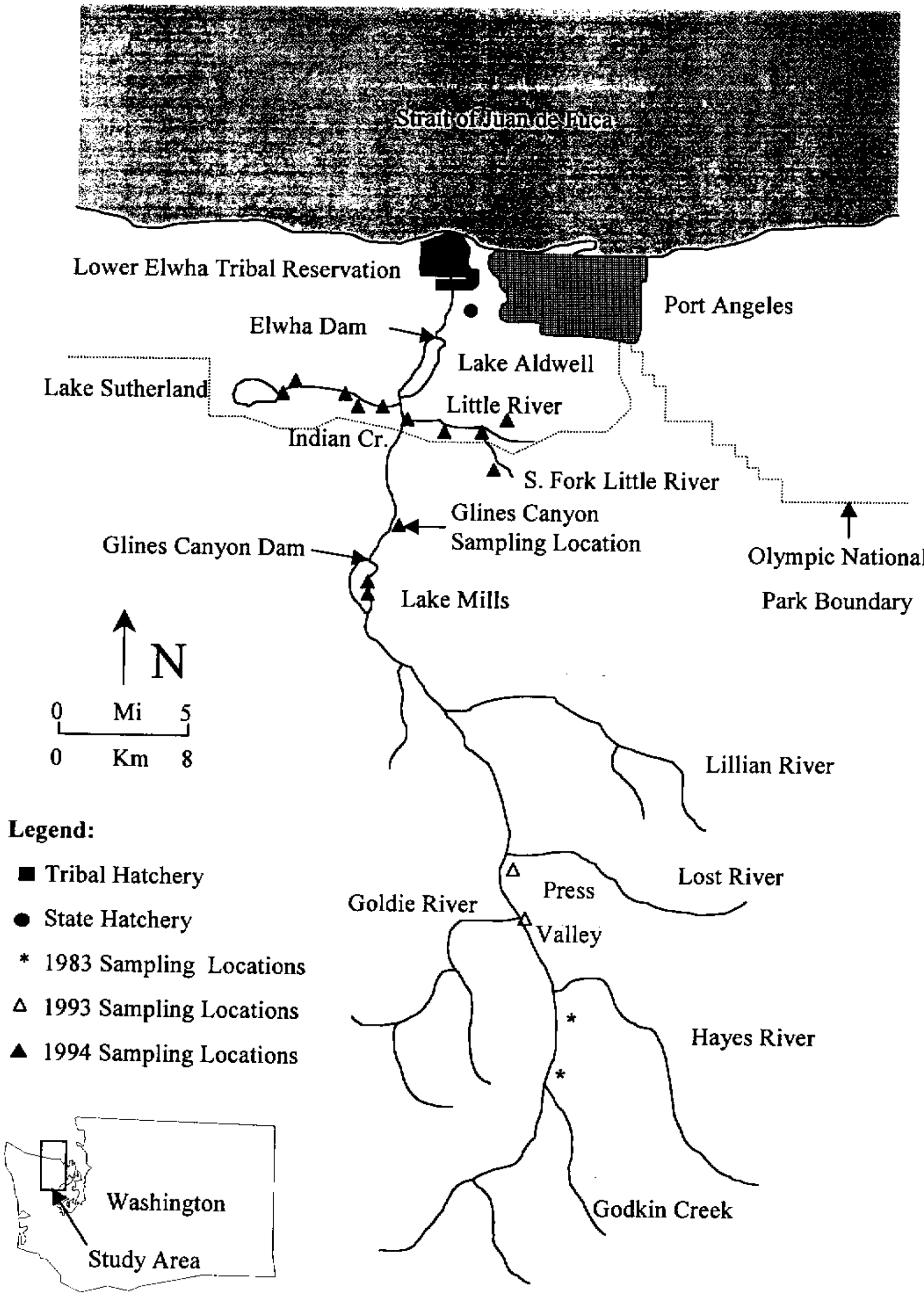

Figure 1. Location where rainbow trout genetic samples were collected in the Elwha River Basin (modified from Wunderlich et al. 1994).

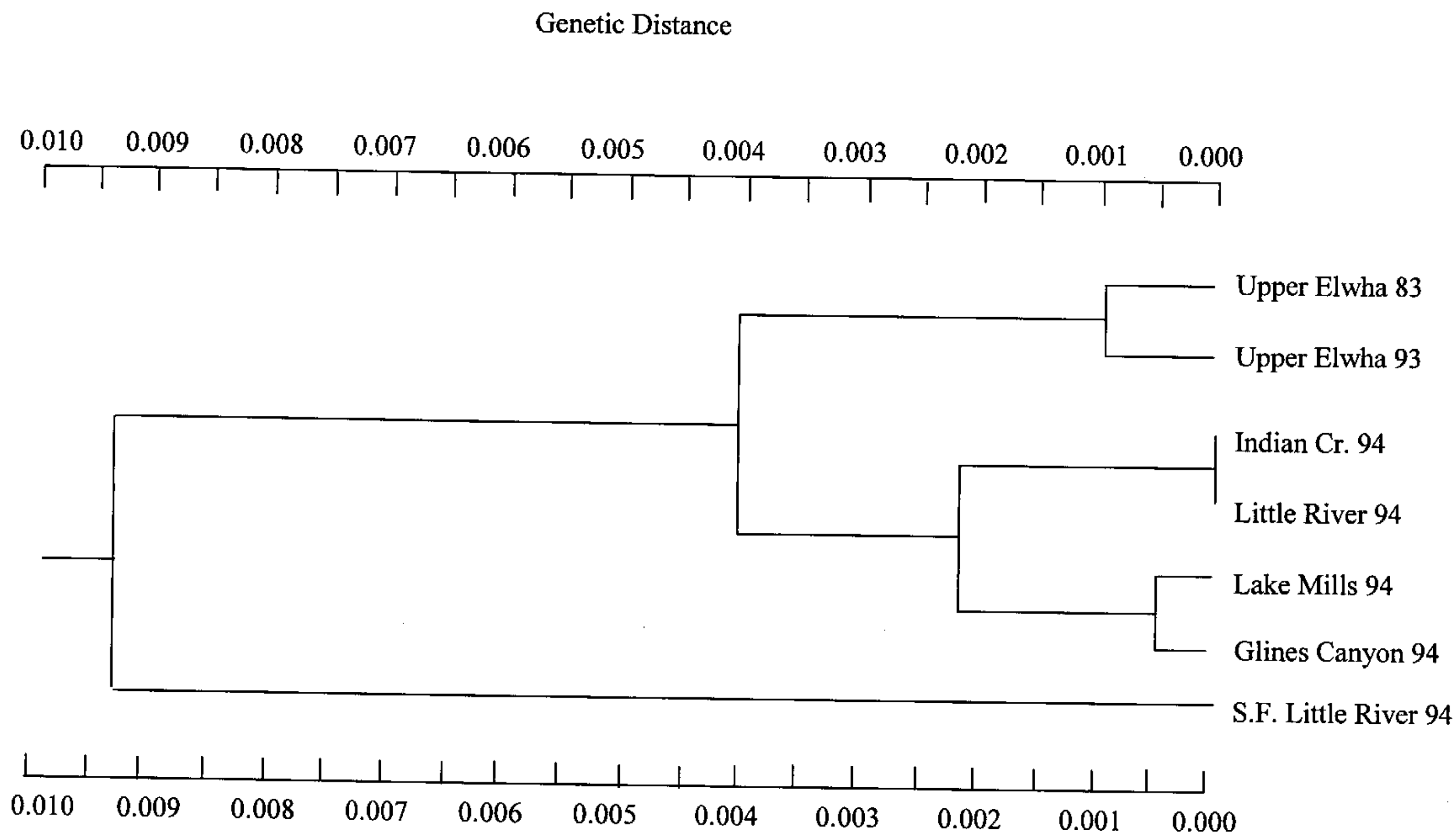

Figure 2. UPGMA dendrogram of Nei's unbiased genetic distance (1978) among rainbow trout collections from the Elwha River based on 18 loci.

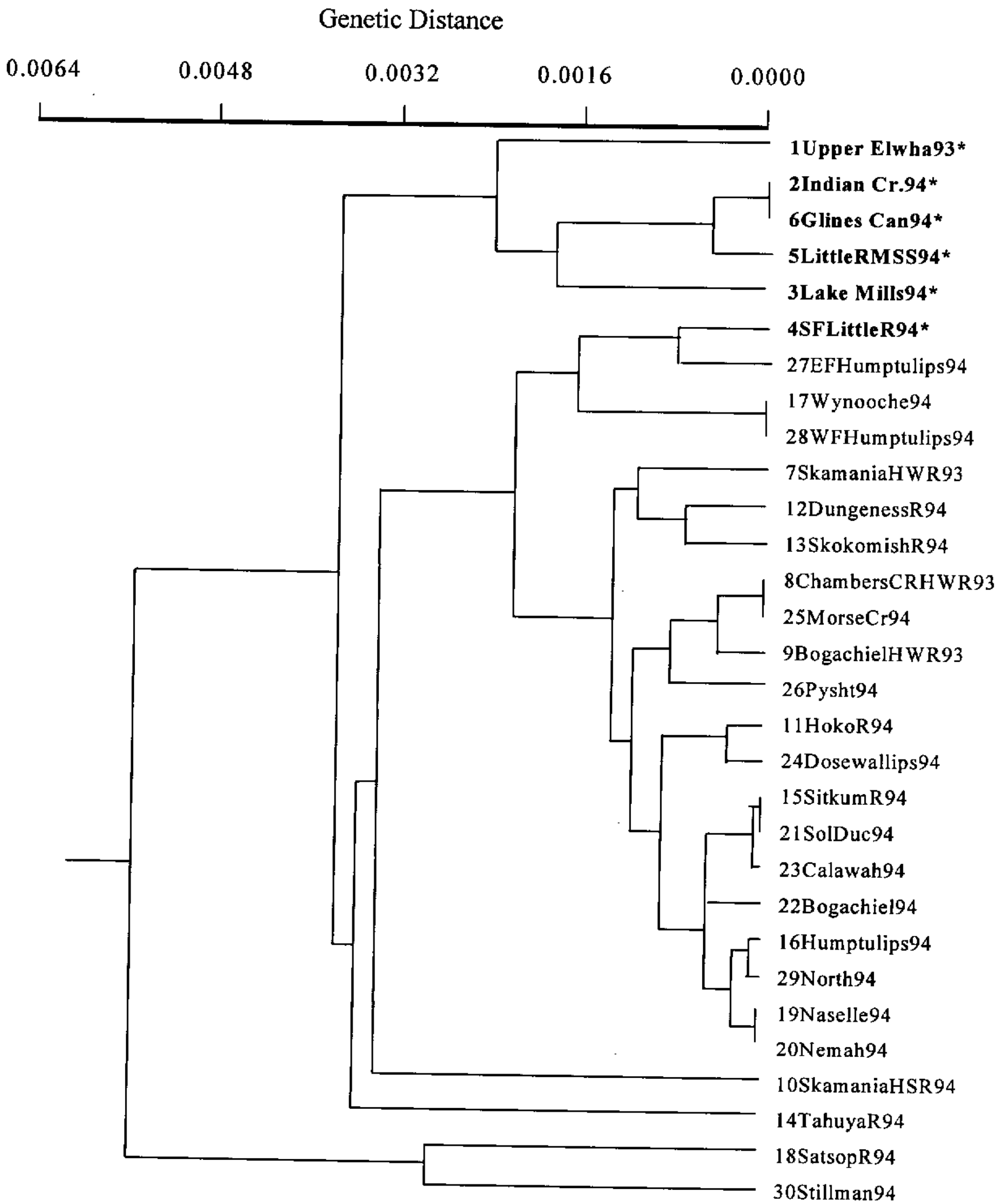

Figure 3. UPGMA dendrogram of Nei's unbiased genetic distance (1978) among six *O. mykiss* collections from the Elwha River (*) and 24 steelhead collections from Washington based on 56 loci.

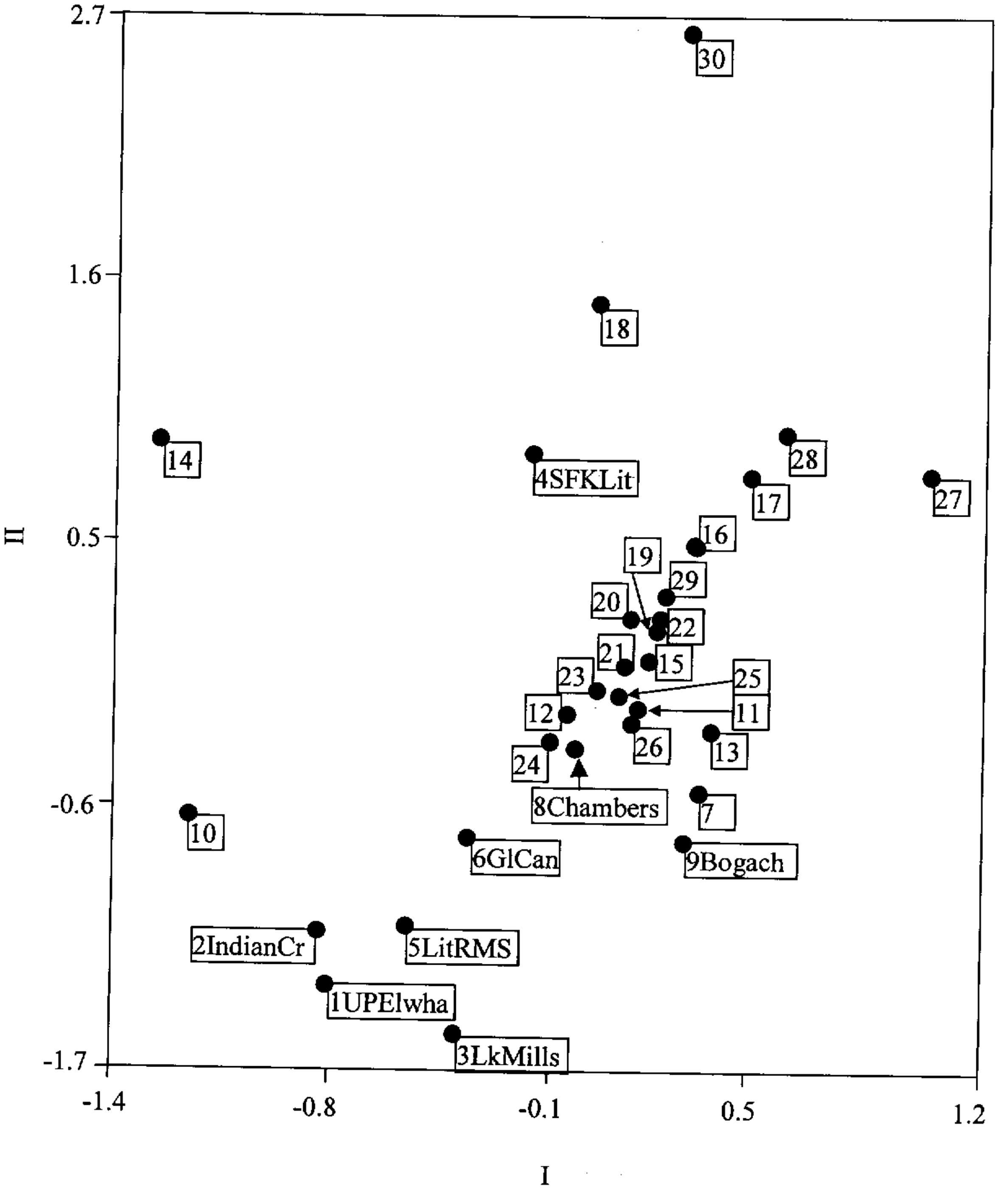

Figure 4. Two dimensional multidimensional scaling plot of Nei's (1978) genetic distance among *O. mykiss* collections from the Elwha River and steelhead collections from Washington based on 56 loci. Numbers within the boxes refer to the numbers and names on the dendrogram in Figure 3. The Elwha River collections and the Chambers Creek Hatchery and Bogachiel Hatchery steelhead points are named in this figure.

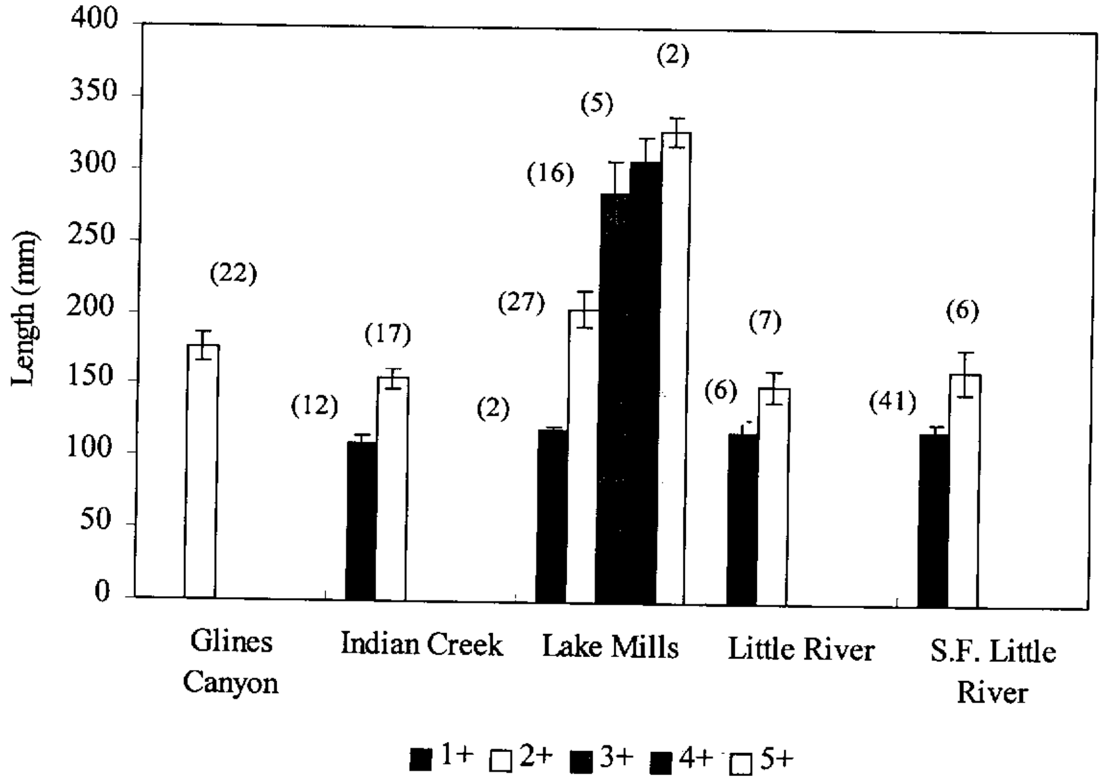

Figure 5. Average length of *O. mykiss* of different age classes (1+ through 5+) present at the 1994 sampling locations. Sample size (n) is listed in parentheses next to the error bars. Error bars represent +/- 2 standard error of the mean.

APPENDIX A. Allele frequencies for variable loci in *O. mykiss* collections from the Elwha River and hatchery and wild steelhead from Washington (Refer to Table 2 for the collection names).

	Collection														
Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
mAAT-1															
(N)	65	29	53	41	14	22	50	50	50	88	50	63	48	61	37
-100	1.000	0.948	0.991	0.951	1.000	0.909	1.000	1.000	0.990	0.972	0.990	0.992	1.000	0.992	1.000
-110	0.000	0.052	0.009	0.049	0.000	0.091	0.000	0.000	0.010	0.028	0.010	0.008	0.000	0.008	0.000
sAAT-1,2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	44
100	1.000	0.978	0.981	1.000	1.000	1.000	0.995	0.990	0.995	1.000	0.996	0.982	0.930	0.996	1.000
112	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000
90	0.000	0.022	0.019	0.000	0.000	0.000	0.005	0.005	0.005	0.000	0.004	0.018	0.070	0.004	0.000
sAAT-3															
(N)	65	33	53	49	13	22	50	50	50	102	54	68	46	63	46
100	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
80	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ADA-1															
(N)	65	33	53	50	15	22	50	50	50	101	54	68	50	63	46
100	0.969	0.864	0.849	1.000	0.967	0.909	1.000	0.980	1.000	1.000	0.972	0.904	0.990	0.992	0.978
69	0.008	0.106	0.085	0.000	0.033	0.045	0.000	0.000	0.000	0.000	0.009	0.015	0.000	0.000	0.000
80	0.023	0.030	0.066	0.000	0.000	0.045	0.000	0.020	0.000	0.000	0.019	0.081	0.010	0.008	0.022
ADA-2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	0.955	1.000	1.000	1.000	0.977	1.000	0.980	0.950	0.995	0.972	0.985	0.990	0.952	1.000
106	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.020	0.050	0.005	0.009	0.015	0.010	0.024	0.000
90	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000
110	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.024	0.000
ADH															
(N)	65	33	53	50	13	22	50	50	50	102	53	68	50	62	38
-100	0.985	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.946	1.000	1.000	1.000	1.000	1.000
-78	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-50	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-171	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.054	0.000	0.000	0.000	0.000	0.000
mAH-1															
(N)	65	33	53	47	11	21	49	48	50	85	54	57	50	61	33
100	1.000	1.000	1.000	1.000	1.000	1.000	0.990	0.979	0.960	1.000	0.991	1.000	1.000	1.000	1.000
55	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.021	0.040	0.000	0.009	0.000	0.000	0.000	0.000
mAH-3															
(N)	65	30	53	45	12	21	50	50	50	85	53	56	50	61	33
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
122	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mAH-4															
(N)	61	30	52	41	10	13	50	50	50	87	52	55	49	60	34
100	0.975	1.000	0.981	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.981	1.000	1.000	0.992	0.956
115	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.008	0.044
83	0.025	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sAH															
(N)	64	33	53	50	13	22	50	50	50	102	54	68	50	62	42
100	0.969	0.894	0.802	0.930	0.846	0.841	0.930	0.820	0.800	0.956	0.833	0.853	0.740	0.871	0.881
85	0.008	0.106	0.142	0.060	0.154	0.091	0.030	0.080	0.130	0.039	0.167	0.118	0.250	0.129	0.119
50	0.023	0.000	0.057	0.010	0.000	0.068	0.040	0.100	0.070	0.005	0.000	0.029	0.010	0.000	0.000
112	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Locus	Collection														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
ALAT															
(N)	65	28	53	48	15	22	50	50	50	102	53	68	50	63	46
100	1.000	1.000	0.981	1.000	1.000	1.000	0.980	0.990	0.970	0.956	1.000	0.993	0.990	0.984	0.967
105	0.000	0.000	0.019	0.000	0.000	0.000	0.020	0.010	0.030	0.044	0.000	0.007	0.010	0.016	0.011
111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
88	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022
CK-A1															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.968
67	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
75	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032
CK-C1															
(N)	58	33	53	49	12	22	49	50	49	102	50	18	45	63	35
100	1.000	1.000	1.000	1.000	1.000	0.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
105	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
98	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CK-C2															
(N)	47	33	52	49	12	21	49	50	46	102	51	13	44	61	30
100	1.000	1.000	1.000	0.990	1.000	1.000	0.990	0.990	1.000	0.990	1.000	1.000	0.989	0.967	0.967
104	0.000	0.000	0.000	0.010	0.000	0.000	0.010	0.010	0.000	0.010	0.000	0.000	0.011	0.033	0.033
FH															
(N)	65	33	53	50	15	22	50	49	50	102	54	68	50	63	46
100	1.000	0.985	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
84	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
119	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GAPDH-3															
(N)	65	31	53	49	13	22	50	49	49	92	53	68	50	60	35
100	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	0.980	1.000	1.000	0.985	0.990	1.000	1.000
33	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.020	0.000	0.000	0.015	0.010	0.000	0.000
bGLUA															
(N)	65	33	52	50	13	22	50	50	50	101	54	68	50	62	43
100	0.992	0.833	0.731	1.000	0.769	0.864	0.980	0.990	1.000	0.995	0.963	0.971	0.990	0.976	0.953
-39	0.000	0.015	0.058	0.000	0.000	0.000	0.020	0.010	0.000	0.005	0.028	0.007	0.000	0.000	0.000
-11	0.008	0.152	0.212	0.000	0.231	0.136	0.000	0.000	0.000	0.000	0.009	0.022	0.010	0.024	0.047
GPI-A															
(N)	65	33	52	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	0.980	0.980	0.950	0.936	1.000	1.000	1.000	1.000	1.000
105	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
93	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.020	0.050	0.064	0.000	0.000	0.000	0.000	0.000
77	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPI-B1															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.989
142	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
153	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPI-B2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000
60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
G3PDH-1															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
-100	1.000	0.985	1.000	1.000	0.967	1.000	0.990	0.970	0.960	0.868	0.991	0.963	0.990	0.992	0.979
80	0.000	0.015	0.000	0.000	0.033	0.000	0.010	0.030	0.040	0.132	0.000	0.037	0.010	0.008	0.021
-150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
40	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000

	Collection														
Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
IDDH-2															
(N)	62	33	52	49	13	19	50	33	49	102	52	68	50	61	41
100	1.000	0.955	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.978	1.000	0.967	0.988
143	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.033	0.000
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012
161	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mIDHP-1															
(N)	65	33	53	50	15	22	50	50	50	102	54	67	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000
-75	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mIDHP-2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	46
100	0.792	0.818	0.726	0.910	0.700	0.864	0.980	0.890	0.890	1.000	0.917	0.919	0.980	0.952	0.870
142	0.008	0.152	0.066	0.000	0.233	0.091	0.000	0.000	0.000	0.000	0.009	0.022	0.000	0.000	0.000
162	0.177	0.030	0.198	0.040	0.067	0.045	0.010	0.060	0.090	0.000	0.056	0.051	0.000	0.040	0.098
67	0.023	0.000	0.009	0.050	0.000	0.000	0.010	0.050	0.020	0.000	0.019	0.007	0.020	0.008	0.033
sIDHP-1															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	62	47
100	0.985	0.939	0.934	1.000	1.000	0.977	1.000	1.000	0.990	0.995	0.981	0.971	0.970	0.976	0.979
121	0.000	0.030	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000
123	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
116	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
74	0.015	0.030	0.047	0.000	0.000	0.023	0.000	0.000	0.000	0.005	0.019	0.029	0.030	0.024	0.021
sIDHP-2															
(N)	65	33	53	50	11	21	50	49	50	102	53	68	49	62	43
100	0.215	0.242	0.264	0.390	0.136	0.190	0.210	0.347	0.230	0.137	0.217	0.140	0.184	0.452	0.209
42	0.177	0.394	0.481	0.230	0.273	0.357	0.410	0.265	0.380	0.490	0.368	0.338	0.327	0.161	0.349
72	0.392	0.288	0.198	0.380	0.455	0.357	0.340	0.316	0.320	0.279	0.321	0.456	0.429	0.371	0.372
123	0.054	0.061	0.038	0.000	0.136	0.024	0.030	0.051	0.070	0.029	0.075	0.066	0.041	0.016	0.058
40	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
58	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.020	0.000	0.012
27	0.162	0.015	0.019	0.000	0.000	0.071	0.010	0.020	0.000	0.064	0.009	0.000	0.000	0.000	0.000
LDH-B2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	0.992	0.939	0.972	0.970	1.000	0.955	0.900	0.840	0.740	0.892	0.861	0.949	0.970	0.849	0.957
76	0.008	0.061	0.028	0.030	0.000	0.045	0.100	0.160	0.260	0.108	0.139	0.051	0.030	0.151	0.043
113	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LDH-C															
(N)	65	33	53	49	13	22	50	50	50	102	54	68	46	63	47
100	0.992	1.000	1.000	1.000	1.000	0.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
95	0.008	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sMDH-A1,2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	0.990	0.985	0.995	1.000	0.996	1.000	0.995	0.996	0.994
155	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
137	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
120	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
49	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.004	0.006
72	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.015	0.005	0.000	0.000	0.000	0.005	0.000	0.000

Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
								Collection							
sMDH-B1,2															
(N)	65	33	53	50	15	22	50	50	50	102	54	67	50	63	47
100	0.946	0.864	0.924	0.790	0.884	0.864	0.940	0.935	0.925	0.897	0.828	0.926	0.925	0.802	0.872
78	0.019	0.068	0.052	0.190	0.084	0.080	0.045	0.045	0.050	0.103	0.148	0.060	0.035	0.123	0.069
116	0.004	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.010	0.004	0.010	0.000	0.010
83	0.031	0.030	0.004	0.020	0.016	0.034	0.015	0.020	0.025	0.000	0.004	0.011	0.030	0.076	0.032
92	0.000	0.038	0.010	0.000	0.016	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
120	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.016
ME															
(N)	65	32	53	50	15	22	50	50	50	100	54	68	48	62	36
100	0.977	0.984	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
110	0.000	0.016	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
87	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mMEP-1															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	46
100	0.992	1.000	1.000	1.000	1.000	1.000	1.000	0.950	0.990	0.995	0.991	1.000	1.000	0.944	1.000
90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
36	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
115	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.010	0.005	0.009	0.000	0.000	0.056	0.000
sMEP-1															
(N)	65	32	53	50	12	22	50	50	50	102	54	68	50	62	46
100	0.992	0.875	0.991	0.890	0.708	0.977	0.820	0.840	0.900	0.951	0.852	0.875	0.880	0.911	0.848
102	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
98	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
83	0.008	0.125	0.009	0.110	0.250	0.023	0.180	0.160	0.100	0.049	0.148	0.125	0.120	0.089	0.152
115	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
93	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
71	0.000	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sMEP-2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	62	42
100	1.000	0.985	1.000	0.990	0.933	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.960	1.000
83	0.000	0.000	0.000	0.000	0.067	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
97	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
105	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.000	0.015	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.000
MPI															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	0.990	1.000	1.000	1.000	1.000	1.000	1.000
95	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
104	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000
NTP															
(N)	63	32	53	50	15	22	50	50	50	101	52	68	50	63	47
100	0.492	0.594	0.321	0.220	0.467	0.477	0.390	0.420	0.430	0.347	0.385	0.294	0.320	0.484	0.213
135	0.508	0.375	0.679	0.780	0.533	0.523	0.610	0.580	0.570	0.653	0.615	0.706	0.680	0.516	0.787
161	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
76	0.000	0.031	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEPA															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	0.955	1.000	0.980	1.000	0.977	1.000	0.990	1.000	0.956	1.000	1.000	0.990	0.968	1.000
122	0.000	0.045	0.000	0.020	0.000	0.023	0.000	0.000	0.000	0.025	0.000	0.000	0.010	0.032	0.000
69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.020	0.000	0.000	0.000	0.000	0.000
PEPB-1															
(N)	62	32	53	49	14	22	50	50	50	99	49	64	50	62	38
100	0.895	0.984	0.943	0.980	0.929	0.955	0.970	0.880	0.860	0.924	0.898	0.977	0.960	0.952	0.908
134	0.000	0.016	0.000	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
69	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-50	0.105	0.000	0.057	0.020	0.036	0.023	0.030	0.120	0.140	0.076	0.102	0.023	0.040	0.048	0.092

	Collection														
Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
PEPD-1															
(N)	65	33	53	50	14	22	50	50	50	100	54	67	50	63	47
100	0.946	0.970	0.943	1.000	0.857	0.977	0.930	0.970	0.970	0.885	0.972	0.918	0.930	0.873	0.979
94	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.054	0.030	0.057	0.000	0.143	0.023	0.070	0.030	0.030	0.115	0.028	0.082	0.070	0.127	0.021
87	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEP-LT															
(N)	65	30	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	1.000	0.991	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.991	1.000	1.000	0.960	1.000
130	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.040	0.000
PGK-2															
(N)	65	33	53	49	11	22	49	50	50	102	54	68	50	63	47
100	0.469	0.439	0.425	0.612	0.409	0.455	0.398	0.420	0.300	0.588	0.407	0.507	0.380	0.492	0.340
115	0.515	0.545	0.547	0.388	0.591	0.523	0.551	0.570	0.670	0.402	0.565	0.493	0.600	0.508	0.660
144	0.015	0.015	0.028	0.000	0.000	0.023	0.051	0.010	0.030	0.010	0.028	0.000	0.020	0.000	0.000
PGM-1															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	45
-100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	0.992	1.000
null	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-85	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.008	0.000
-140	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-95	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PGM-2															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
-100	1.000	0.970	1.000	1.000	1.000	0.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.992	0.968
-120	0.000	0.030	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.011
200	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
PNP															
(N)	65	33	53	47	11	20	50	50	50	100	50	61	23	61	38
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.970	0.980	1.000	1.000	1.000	1.000	1.000	1.000
107	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.020	0.000	0.000	0.000	0.000	0.000	0.000
mSOD															
(N)	65	31	53	50	13	22	50	50	50	101	54	68	11	56	36
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
124	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
81	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sSOD-1															
(N)	65	33	53	50	13	22	50	50	50	102	54	67	50	63	47
100	0.831	0.773	0.821	0.670	0.846	0.750	0.480	0.620	0.570	0.804	0.602	0.664	0.550	0.429	0.670
152	0.169	0.227	0.179	0.330	0.154	0.250	0.520	0.380	0.430	0.196	0.398	0.336	0.450	0.571	0.330
38	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
148	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
TPI-3															
(N)	65	33	53	50	15	22	50	50	50	102	54	68	50	63	47
100	1.000	0.939	1.000	0.960	0.933	0.955	1.000	1.000	1.000	0.995	0.991	1.000	0.990	0.976	0.968
94	0.000	0.030	0.000	0.010	0.000	0.045	0.000	0.000	0.000	0.005	0.009	0.000	0.010	0.024	0.032
102	0.000	0.030	0.000	0.030	0.067	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

APPENDIX A cont. Allele frequencies in collections 16 thru 30

	Collection														
Locus	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
mAAT-1															
(N)	44	29	19	36	36	45	51	45	1	1	27	20	1	38	45
-100	1.000	1.000	1.000	0.986	0.986	0.989	1.000	0.989	1.000	1.000	1.000	1.000	1.000	0.987	1.000
-110	0.000	0.000	0.000	0.014	0.014	0.011	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.013	0.000
sAAT-1,2															
(N)	50	51	64	45	44	52	51	52	49	49	50	50	50	49	49
100	0.995	1.000	1.000	1.000	1.000	0.995	0.980	0.981	1.000	0.995	1.000	1.000	1.000	0.995	1.000
112	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.014	0.000	0.005	0.000	0.000	0.000	0.000	0.000
90	0.005	0.000	0.000	0.000	0.000	0.000	0.020	0.005	0.000	0.000	0.000	0.000	0.000	0.005	0.000
sAAT-3															
(N)	50	51	64	45	44	52	51	52	50	50	50	50	50	49	49
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
80	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ADA-1															
(N)	50	51	64	45	44	52	51	52	48	49	50	48	48	49	49
100	0.990	1.000	1.000	1.000	1.000	0.962	1.000	0.981	0.979	0.980	0.960	1.000	0.990	0.949	1.000
69	0.010	0.000	0.000	0.000	0.000	0.038	0.000	0.000	0.021	0.010	0.020	0.000	0.010	0.000	0.000
80	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.010	0.020	0.000	0.000	0.051	0.000
ADA-2															
(N)	50	51	64	45	44	40	51	52	51	46	50	47	48	49	49
100	0.920	0.941	0.852	0.978	0.966	1.000	0.931	1.000	1.000	1.000	0.980	0.872	0.969	0.969	0.949
106	0.070	0.059	0.148	0.022	0.034	0.000	0.029	0.000	0.000	0.000	0.010	0.128	0.031	0.031	0.051
90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000
110	0.010	0.000	0.000	0.000	0.000	0.000	0.039	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ADH															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	47	37
-100	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
-78	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-50	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-171	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mAH-1															
(N)	48	51	56	45	44	52	51	52	31	42	50	44	48	49	48
100	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000
55	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000
mAH-3															
(N)	47	51	57	45	44	52	51	51	32	42	50	41	48	49	48
100	0.989	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
122	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mAH-4															
(N)	47	51	55	45	44	52	50	51	32	42	50	41	48	49	47
100	1.000	1.000	1.000	1.000	1.000	1.000	0.970	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
115	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
83	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sAH															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	47	48
100	0.780	0.843	0.922	0.933	0.886	0.923	0.922	0.856	0.802	0.740	0.800	0.850	0.750	0.851	0.719
85	0.200	0.127	0.063	0.056	0.114	0.058	0.049	0.144	0.170	0.160	0.180	0.120	0.250	0.085	0.281
50	0.020	0.029	0.016	0.011	0.000	0.019	0.020	0.000	0.028	0.100	0.020	0.030	0.000	0.064	0.000
112	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Locus	Collection														
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
ALAT															
(N)	50	51	64	44	44	52	51	25	1	1	26	29	1	48	49
100	0.990	1.000	1.000	1.000	1.000	0.981	1.000	1.000	1.000	1.000	0.981	0.948	1.000	0.979	0.980
105	0.010	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.019	0.052	0.000	0.021	0.020
111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
88	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CK-A1															
(N)	50	51	64	44	44	52	51	52	53	50	47	48	49	49	49
100	0.990	1.000	1.000	1.000	1.000	1.000	1.000	0.981	1.000	1.000	1.000	1.000	0.990	1.000	1.000
67	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
75	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.010	0.000	0.000
CK-C1															
(N)	50	51	64	44	44	52	51	52	50	50	50	49	50	49	49
100	1.000	0.980	0.984	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.959
105	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
98	0.000	0.020	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.041
CK-C2															
(N)	49	49	58	44	44	52	51	37	49	49	49	46	49	49	49
100	0.969	0.949	0.922	1.000	0.966	1.000	1.000	0.986	1.000	0.980	1.000	0.946	0.908	0.990	0.990
104	0.031	0.051	0.078	0.000	0.034	0.000	0.000	0.014	0.000	0.020	0.000	0.054	0.092	0.010	0.010
FH															
(N)	49	51	63	44	44	50	51	52	52	50	47	48	49	49	49
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
84	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
119	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GAPDH-3															
(N)	48	51	61	44	44	52	51	52	53	50	47	49	50	48	37
100	0.969	0.990	1.000	1.000	0.989	1.000	0.971	1.000	1.000	0.990	1.000	1.000	0.980	0.969	1.000
33	0.031	0.010	0.000	0.000	0.011	0.000	0.029	0.000	0.000	0.010	0.000	0.000	0.020	0.031	0.000
bGLUA															
(N)	50	51	62	45	43	52	49	52	52	50	49	50	49	44	37
100	0.990	0.980	1.000	1.000	1.000	0.942	0.990	0.962	0.981	0.990	1.000	0.970	1.000	0.977	0.946
-39	0.010	0.020	0.000	0.000	0.000	0.010	0.000	0.000	0.019	0.010	0.000	0.030	0.000	0.011	0.041
-11	0.000	0.000	0.000	0.000	0.000	0.048	0.010	0.038	0.000	0.000	0.000	0.000	0.000	0.011	0.014
GPI-A															
(N)	50	51	64	44	44	52	51	52	53	50	47	48	48	49	49
100	1.000	0.980	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	0.990	1.000	0.959
105	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.010
93	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
77	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.031
GPI-B1															
(N)	50	51	64	44	44	52	51	52	53	50	47	48	49	49	49
100	0.990	1.000	0.992	1.000	0.989	1.000	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
142	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
153	0.010	0.000	0.008	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPI-B2															
(N)	50	51	64	44	44	52	51	52	53	50	47	48	49	49	49
100	1.000	1.000	1.000	0.989	1.000	0.971	1.000	1.000	0.991	1.000	1.000	1.000	1.000	1.000	1.000
60	0.000	0.000	0.000	0.011	0.000	0.029	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000
G3PDH-1															
(N)	50	51	64	45	44	52	51	52	53	42	47	48	49	49	49
-100	0.980	0.980	0.906	0.956	1.000	0.933	0.951	0.990	1.000	1.000	0.989	0.990	0.949	0.908	0.847
80	0.020	0.020	0.086	0.011	0.000	0.067	0.039	0.010	0.000	0.000	0.011	0.010	0.051	0.041	0.082
-150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
40	0.000	0.000	0.008	0.033	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.051	0.071

Locus	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
	Collection														
IDDH-2															
(N)	50	51	61	44	44	52	50	52	53	49	50	49	49	47	35
100	0.980	1.000	0.967	1.000	0.989	1.000	1.000	1.000	0.991	1.000	0.980	0.969	1.000	1.000	0.986
143	0.010	0.000	0.033	0.000	0.011	0.000	0.000	0.000	0.009	0.000	0.020	0.031	0.000	0.000	0.014
5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
161	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mIDHP-1															
(N)	50	51	64	44	44	52	51	52	52	49	47	47	48	49	49
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.918	1.000	1.000	1.000	1.000	1.000
-75	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.082	0.000	0.000	0.000	0.000	0.000
mIDHP-2															
(N)	50	51	64	45	44	52	50	52	53	50	50	49	48	49	49
100	0.940	0.961	0.938	0.900	0.966	0.913	0.920	0.856	0.906	0.910	0.860	0.898	0.938	0.969	0.969
142	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
162	0.050	0.020	0.063	0.078	0.034	0.058	0.060	0.096	0.057	0.060	0.110	0.020	0.063	0.031	0.020
67	0.010	0.020	0.000	0.022	0.000	0.029	0.020	0.048	0.038	0.030	0.030	0.082	0.000	0.000	0.010
sIDHP-1															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	49
100	0.960	0.971	0.984	0.967	1.000	1.000	0.971	0.990	0.915	0.990	0.960	0.960	0.980	0.980	1.000
121	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.010	0.000
123	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
116	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000
74	0.040	0.029	0.016	0.033	0.000	0.000	0.029	0.010	0.075	0.010	0.030	0.040	0.020	0.010	0.000
sIDHP-2															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	49
100	0.290	0.314	0.242	0.322	0.250	0.221	0.275	0.279	0.151	0.280	0.290	0.270	0.250	0.286	0.265
42	0.260	0.265	0.242	0.322	0.239	0.365	0.314	0.317	0.377	0.280	0.250	0.270	0.320	0.265	0.235
72	0.340	0.382	0.438	0.267	0.420	0.404	0.333	0.327	0.311	0.320	0.300	0.410	0.430	0.367	0.378
123	0.110	0.039	0.078	0.067	0.080	0.010	0.069	0.077	0.057	0.100	0.160	0.050	0.000	0.082	0.122
40	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
58	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.085	0.000	0.000	0.000	0.000	0.000	0.000
27	0.000	0.000	0.000	0.022	0.011	0.000	0.010	0.000	0.019	0.020	0.000	0.000	0.000	0.000	0.000
LDH-B2															
(N)	50	51	64	45	44	52	50	52	53	50	50	50	50	49	49
100	0.930	0.961	0.984	0.900	0.909	0.904	0.830	0.971	0.943	0.850	0.850	0.970	0.980	0.939	1.000
76	0.070	0.039	0.016	0.078	0.080	0.096	0.170	0.029	0.057	0.150	0.150	0.030	0.020	0.061	0.000
113	0.000	0.000	0.000	0.022	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LDH-C															
(N)	50	51	64	45	44	52	51	52	50	50	50	50	50	49	49
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000
95	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000
sMDH-A1,2															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	49
100	1.000	0.980	0.992	1.000	0.988	0.986	0.970	1.000	0.976	0.975	0.985	1.000	0.990	0.984	1.000
155	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
37	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
120	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000
49	0.000	0.014	0.000	0.000	0.000	0.000	0.024	0.000	0.024	0.010	0.000	0.000	0.010	0.000	0.000
72	0.000	0.005	0.008	0.000	0.000	0.014	0.005	0.000	0.000	0.005	0.015	0.000	0.000	0.000	0.000

Locus	Collection 16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
sMDH-B1,2															
(N)	50	51	64	45	44	52	51	50	50	49	50	50	50	49	49
100	0.855	0.853	0.816	0.894	0.909	0.846	0.878	0.880	0.880	0.903	0.910	0.800	0.830	0.842	0.898
78	0.125	0.132	0.176	0.106	0.091	0.110	0.098	0.090	0.085	0.076	0.080	0.200	0.170	0.158	0.102
116	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.005	0.000	0.000	0.000	0.000	0.000
83	0.010	0.014	0.008	0.000	0.000	0.034	0.024	0.015	0.030	0.005	0.010	0.000	0.000	0.000	0.000
92	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
120	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.015	0.000	0.010	0.000	0.000	0.000	0.000	0.000
ME															
(N)	50	51	64	45	44	52	51	49	26	32	50	48	44	49	49
100	1.000	1.000	1.000	1.000	1.000	1.000	0.980	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
110	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
87	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
mMEP-1															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	49
100	1.000	0.980	1.000	0.978	0.977	1.000	1.000	0.990	0.962	0.980	0.980	1.000	0.980	1.000	1.000
90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
36	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
115	0.000	0.020	0.000	0.022	0.023	0.000	0.000	0.010	0.038	0.020	0.020	0.000	0.020	0.000	0.000
sMEP-1															
(N)	50	51	64	45	44	52	51	52	53	50	49	50	50	49	49
100	0.710	0.647	0.609	0.733	0.761	0.846	0.794	0.856	0.830	0.890	0.908	0.800	0.730	0.827	0.439
102	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
98	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
83	0.290	0.353	0.391	0.267	0.239	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
115	0.000	0.000	0.000	0.000	0.000	0.154	0.206	0.144	0.151	0.110	0.092	0.200	0.270	0.173	0.561
93	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
71	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000
sMEP-2															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	48
100	0.990	1.000	1.000	1.000	1.000	1.000	0.951	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
83	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
97	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
105	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.010	0.000	0.000	0.000	0.000	0.000	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MPI															
(N)	50	51	64	45	44	52	51	52	50	50	50	50	50	49	49
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
95	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
104	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
NTP															
(N)	50	50	64	43	44	51	51	52	53	50	45	46	49	49	49
100	0.220	0.160	0.164	0.256	0.307	0.304	0.284	0.337	0.434	0.330	0.256	0.163	0.163	0.204	0.173
135	0.780	0.840	0.836	0.744	0.693	0.696	0.716	0.663	0.566	0.670	0.744	0.837	0.837	0.796	0.827
101	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
76	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEPA															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	49
100	1.000	0.980	1.000	1.000	1.000	1.000	0.961	1.000	1.000	1.000	0.980	1.000	1.000	1.000	1.000
122	0.000	0.020	0.000	0.000	0.000	0.000	0.039	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000
69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEPB-1															
(N)	46	51	42	45	42	51	49	49	49	42	50	47	48	40	21
100	0.891	0.971	1.000	0.889	0.964	0.873	0.847	0.949	0.980	0.917	0.790	0.968	0.906	0.875	1.000
134	0.000	0.000	0.000	0.000	0.000	0.010	0.031	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-50	0.109	0.029	0.000	0.111	0.036	0.118	0.122	0.051	0.020	0.083	0.210	0.032	0.094	0.125	0.000

Locus	Collection 16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
PEPD-1															
(N)	50	51	64	44	44	52	51	52	53	50	47	50	50	48	49
100	0.980	1.000	1.000	0.955	0.989	0.981	0.902	0.990	0.991	0.920	0.904	1.000	1.000	0.969	1.000
94	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
110	0.010	0.000	0.000	0.045	0.011	0.019	0.098	0.010	0.009	0.080	0.096	0.000	0.000	0.031	0.000
87	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PEP-LT															
(N)	50	51	64	44	44	52	51	52	53	41	47	48	49	49	49
100	0.980	0.980	1.000	0.977	0.977	1.000	1.000	1.000	1.000	0.988	1.000	0.969	0.969	0.980	0.980
130	0.020	0.020	0.000	0.023	0.023	0.000	0.000	0.000	0.000	0.012	0.000	0.031	0.031	0.020	0.020
PGK-2															
(N)	50	51	64	45	44	52	51	52	52	50	50	44	49	49	49
100	0.500	0.363	0.328	0.367	0.409	0.356	0.402	0.385	0.481	0.430	0.500	0.511	0.398	0.398	0.286
115	0.500	0.608	0.672	0.600	0.545	0.644	0.598	0.606	0.510	0.550	0.470	0.477	0.602	0.571	0.714
144	0.000	0.029	0.000	0.033	0.045	0.000	0.000	0.010	0.010	0.020	0.030	0.011	0.000	0.031	0.000
PGM-1															
(N)	50	51	64	44	43	52	51	52	53	50	45	47	49	49	49
-100	1.000	1.000	1.000	1.000	1.000	1.000	0.971	1.000	0.981	0.990	1.000	1.000	1.000	1.000	1.000
null	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-85	0.000	0.000	0.000	0.000	0.000	0.000	0.029	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000
-140	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
-95	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
PGM-2															
(N)	50	51	64	45	44	52	51	51	53	50	50	50	50	49	49
-100	1.000	1.000	1.000	0.989	1.000	0.981	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
-120	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
200	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PNP															
(N)	47	48	25	43	27	7	51	51	47	48	44	50	48	40	45
100	0.979	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000
107	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
mSOD															
(N)	48	51	61	45	44	52	51	51	32	50	50	29	1	49	36
100	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
124	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
81	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sSOD-1															
(N)	50	51	64	45	44	52	51	52	53	50	50	50	50	49	49
100	0.680	0.598	0.852	0.644	0.648	0.615	0.578	0.635	0.670	0.610	0.640	0.760	0.610	0.673	0.612
152	0.320	0.382	0.148	0.322	0.352	0.385	0.402	0.356	0.330	0.390	0.360	0.240	0.390	0.327	0.388
38	0.000	0.000	0.000	0.033	0.000	0.000	0.020	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
148	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
TPI-3															
(N)	39	51	64	44	44	52	51	50	48	50	50	50	49	49	49
100	0.962	0.961	0.969	0.989	1.000	0.962	0.902	0.980	0.979	0.990	1.000	0.890	0.959	1.000	1.000
94	0.038	0.039	0.031	0.011	0.000	0.029	0.098	0.020	0.000	0.000	0.000	0.100	0.041	0.000	0.000
102	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.021	0.010	0.000	0.010	0.000	0.000	0.000